Global versus local processing of frequency-modulated tones in gerbils: An animal model of lateralized auditory cortex functions

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Edited by Mortimer Mishkin, National Institutes of Health, Bethesda, MD, and approved February 28, 2008 (received for review August 22, 2007)

Hemispheric asymmetries of speech and music processing might arise from more basic specializations of left and right auditory cortex (AC). It is not clear, however, whether such asymmetries are unique to humans, i.e., consequences of speech and music, or whether comparable lateralized AC functions exist in nonhuman animals, as evolutionary precursors. Here, we investigated the cortical lateralization of perception of linearly frequency-modulated (FM) tones in gerbils, a rodent species with human-like low-frequency hearing. Using a footshock-reinforced shuttle-box avoidance go/no-go procedure in a total of 178 gerbils, we found that (i) the discrimination of direction of continuous FM (rising versus falling sweeps, 250-ms duration) was impaired by right but not left AC lesions; (ii) the discrimination of direction of segmented FM (50-ms segments, 50-ms silent gaps, total duration 250 ms) was impaired by bilateral but not unilateral AC lesions; (iii) the discrimination of gap durations (10–30 ms) in segmented FM was impaired by left but not right AC lesions. AC lesions before and after training resulted in similar effects. Together, these experiments suggest that right and left AC, even in rodents, use different strategies in analyzing FM stimuli. Thus, the right AC, by using global cues, determines the direction of continuous and segmented FM but cannot discriminate gap durations. The left AC, by using local cues, discriminates gap durations and determines FM direction only when additional segmental information is available.

asymmetry | lateralization | rodents

The cerebral lateralization of speech and music processing has remained a persistent puzzle, in particular with regard to the question of which mechanistic level between acoustic-feature analysis and cognitive interpretation of semantic contents may be at the roots of channeling the information to the two hemispheres (1–4). If one entertains a basic auditory hypothesis, it is reasonable to assume that early auditory cortex (AC) should show signs of relevant lateralization and that specializations also apply to some sounds that are clearly not speech or music because their elementary acoustic structure is not unique. In this vein, a rich literature has accumulated supporting the view that right AC may be more prone to high spectral resolution and left AC to high temporal resolution (5–9). There is much evidence indicating that the left AC is specialized for processing rapidly changing sounds, regardless of whether speech or nonspeech (10–13). In support of a causal connection to speech processing, there are a number of studies showing temporal processing deficits in language-impaired children (14, 15) or dyslexic adults (16, 17), and some of these studies indicate that these deficits can be overcome by training (14, 17). Corresponding to the genetic basis of speech and language (18), brain imaging studies showed that in infants a few months old (19) and even in neonates (20), i.e., well before the onset of speech production, there is a left-hemisphere superiority to process specific properties of speech. Recently, Benasich *et al.* (21) used the 6-month old infant as a prelinguistic model to predict later language abilities. Considering these data suggesting that basic auditory processing abilities may underlie human language development, it is sur-

prising that “prelinguistic” animal models do not play a more dominant role in research on auditory cortex functions in humans. This might reflect a widely held belief that human speech and language represent processes unique to humans and, as such, are not amenable to study in nonhuman species (22). Nevertheless, the advantage of animal models is fairly straightforward (23): In humans, speech perception involves both auditory pattern analysis and speech-specific higher levels of processing, dispositions that may not be separable even by studying infants. Animals, however, can provide a model of human’s auditory-level processing in the absence of semantic interference of speech in a search for basic lateralizations of function. But some type of animal research may entail the same semantic problems as human studies with speech. Thus, in the studies using species-specific vocalization in birds (24–26), mice (27, 28), sea lions (29), and monkeys (30–35), as a rule, a left-hemisphere advantage (25, 27–32, 34), and in few studies a right-hemisphere advantage (26, 35), was found—but no asymmetry (24, 29, 33, 35) or a right-hemisphere bias (32, 34) when non-species-specific sounds were applied [for review of animal studies, see supporting information (SI) Table S1]. Therefore, some authors concluded that the laterality effect is related to the communicative valence of signals rather than to their acoustic characteristics (36). Studies applying different artificial, semantically neutral sounds, only occasionally performed in animals (Table S1), yielded inconsistent results (34, 37–41).

Searching for possible precursors of human AC lateralizations in animals, we found that the discrimination of direction of linearly frequency-modulated (FM) tones is impaired by right but not by left AC lesions in gerbils (42). This AC asymmetry has recently been confirmed in rats (43). In human functional (f)MRI experiments, we found that the categorization of direction of FM stimuli produced dominant blood-oxygen level-dependent (BOLD) activation of right AC, but categorization of their duration resulted in activation of left AC (44). Moreover, a matching-to-sample task with the same FM stimuli in serial comparisons generated dominant left AC activations (45). Similarly, in a “streaming” task, where the selective segmental comparison of stimuli is crucial, BOLD activation was lateralized to the left AC (46). This led to the hypothesis that, at least for stimuli with no primary semantic valence, their dominant representation in either right or left AC will depend on the type of task that is executed with them. Thus, the selective use of the cues for comparisons or conceptualizations appears to deter-

Author contributions: W.W., F.W.O., and H.S. designed research; W.W. and F.W.O. analyzed data; and W.W. and H.S. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Freely available online through the PNAS open access option.

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This article contains supporting information online at www.pnas.org/cgi/data/0707844105/DCSupplemental.

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FM tone stimuli

▼, impairment by bilateral lesion; ▼!, impairment by unilateral lesion; O, no effect; *n*, number of animals.
contin., continuous; segm., segmented; Bilat, bilateral.
*The same animals were used in tasks C and D.

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Fig. 4. Effect of unilateral AC lesions on discrimination of gap durations in segmented FM sweeps: Three representative examples of the correlation between gap duration and number of nonreinforced conditioned responses in test sessions of experiments shown in Fig. 3. In *A* and *B*, CS^+ with 50-ms gaps and CS^- with no gaps were used; in *C*, CS^+ with no gaps and CS^- with 50-ms gaps were used as reinforced stimuli. (*A*) Gap-duration discrimination in left and right AC-lesioned animals (test session no. 7 in Fig. 3C): Only in LesR animals, i.e., with left AC intact, responses vary with gap duration. LesL, $r = 0.1785$, $P = 0.672$; LesR, $r = 0.9358$, $P = 0.0006$. (*B*) Gap duration discrimination in session no. 7 (before lesion, gray) and in session no. 17 (after lesion, black) in left and right AC-lesioned animals (from Fig. 3D): After lesion, responses vary with gap duration when left AC is intact. Session no. 7: LesL, $r = 0.7835$, $P = 0.0214$; LesR, $r = 0.8328$, $P = 0.0103$; session no. 17: LesL, $r = 0.1011$, $P = 0.8117$; LesR, $r = 0.8643$, $P = 0.0056$. (*C*) Gap-duration discrimination in session no. 7 (before lesion, gray) and in session no. 17 (after lesion, black) in left and right AC-lesioned animals (from Fig. 3E): Dependence of responses on gap duration with intact left AC like in Fig. 4*A* and *B* but reversed correlation because of CS reversal. Session no. 7: LesL, $r = 0.8718$, $P = 0.0048$; LesR, $r = 0.8549$, $P = 0.0068$; session no. 17: LesL, $r = 0.0869$, $P = 0.8377$; LesR, $r = 0.7111$, $P = 0.0480$.

bilaterally lesioned cases, in unilaterally lesioned animals, the performance in the first training period after the lesion was significantly lower than in control animals, but there was no difference between right and left AC-lesioned groups (compare Fig. 3*C* with *A*, and compare *D* and *E* with *B*). Further details on statistical analysis of discrimination performance can be found in *Results* in *SI Text* and *Table S2*.

Thus, unilaterally lesioned animals showed no hemisphere-specific impairment when the average performance to the trained FM stimuli was measured (difference between hit rate and false alarms). As shown in Fig. 3, intermediate testing with shorter untrained gaps always lowered the discrimination performance per session in control and lesioned animals. This drop of performance also showed no significant right/left-hemisphere difference. Such a difference, however, appeared when we used the average conditioned response rates and plotted them as a function of gap duration (10–30 ms) of the untrained, i.e., nonreinforced test FM. Fig. 4*A–C* shows three examples of this correlation analysis for the before and after training and lesion groups of Fig. 3*C*, *D*, and *E*, respectively. Animals with intact left AC systematically changed the conditioned response rate with gap duration both after before-training (Fig. 4*A*) and after-training (Fig. 4*B* and *C*) lesions. Animals with only right AC intact responded similarly for all gaps, i.e., showed no dependence of conditioned response rate on gap duration.

The positive and negative slopes of the regression lines in Fig. 4*A–C* have an interesting implication: They allow an interpretation as psychophysical generalization gradients. In the group in which the segmented FM with 50-ms gaps during training was used as a CS^+ (Figs. 3*C* and *D* and 4*A* and *B*) the highest conditioned response rate to the test FM occurred with longest gaps (30 ms). In the group with continuous FM used as a CS^+ (Figs. 3*E* and 4*C*), the highest conditioned response rate to the test FM occurred with shortest gaps (10 ms). Thus, segmental generalization that depends on the left hemisphere uses similarities to the trained CS as a cue. Fig. 5, summarizing the results of all test sessions in all groups of experiment 3, shows that there is a significant correlation between gap duration and conditioned responses in controls and in right AC-lesioned gerbils but not in bilateral or left AC-lesioned gerbils.

Experiments 1, 2, and 3 together (see Table 1) suggest the following strategies of AC lateralization: The right AC is not sensitive to segmental variation and therefore might be able to disregard any segmentation for determining the direction of FM. It seems to generate a rather global view of direction of

frequency change. The left AC, by contrast, seems to rely on segmentations to determine and distinguish directions of frequency change. Its dependence on the local spectrotemporal cues of segmentations is so strong that it does not consider variations of a learned segmentation as equivalent, even though the periodicity of segments at 10 Hz and the total frequency bandwidth of the FM remained the same in all cases.

Discussion

Our results demonstrate a high degree of asymmetry of right and left AC processing of artificial sounds by using FM directional discrimination and FM gap-duration discrimination tasks in a nonhuman species. Direct evidence of hemispheric asymmetries in studies using artificial sounds were found hitherto mostly in humans. In these studies, which used different auditory nonspeech stimuli that varied in temporal and spectral domains, either a left-hemispheric or a right-hemispheric dominance was found depending on the acoustic characteristics of stimuli (5, 6, 8, 9, 11, 13). These human studies suggest that hemispheric asymmetry is not merely a speech-specific phenomenon as originally assumed but

Fig. 5. Gap-duration discrimination in AC-lesioned animals: Correlation between gap duration and number of nonreinforced responses in test sessions before and after unilateral or bilateral AC lesions (as illustrated in three examples in Fig. 4) calculated from all experiments shown in Fig. 3. Each correlation coefficient was calculated from four gap-duration test sessions either before (hatched columns) or after (black columns) lesions. Les, bilateral lesion; SL, sham-lesion; LesL, lesion left; LesR, lesion right; hatched line: significance level ($r = 0.3494$; $P = 0.05$); *, $P < 0.01$; **, $P < 0.001$; ***, $P < 0.0001$. (*A*) Bilateral and unilateral lesions before training (Fig. 3*A* and *C*). (*B*) Bilateral and unilateral lesions after training (Fig. 3*B* and *D*). In *A* and *B*, CS^+ with gaps of 50 ms and CS^- with no gaps were used. (*C*) Unilateral lesions after training (Fig. 3*E*). In this case, CS^+ had no gaps, and CS^- had gaps of 50 ms.

Fig. 6. Autoradiographs (2-fluoro-2-deoxy-D-[^{14}C (U)]-glucose) of horizontal sections through the gerbil brain. Anterior and posterior borders of auditory cortex (AC) are indicated by broken lines. The solid line indicates a rostrocaudal reference coordinate that corresponds to the anterior tips of hippocampi. Shown is a brain section from a sham-lesioned animal (A) and representative examples of a small (B) and a big (C) unilateral AC lesion. AAF, anterior auditory field; AI, auditory field AI; DP/VP, dorsoposterior and ventroposterior auditory fields.

rather depends on temporal vs. spectral (5–8), rapid vs. slow (51), and/or local vs. global (52, 53) processing of any auditory stimuli. The present animal data on lateralized auditory cortex functions in gerbils are consistent with this view. An overview of our data, containing the different acoustic stimuli, the discrimination tasks, and the unilateral and bilateral lesion effects in all experimental series of the present study, is given in Table 1. These AC lesion studies suggest not only that right or left AC are superior to the other hemisphere in the performance of one or another discrimination task, i.e., fulfill a dominance criterion but are sufficient to execute different tasks. Within the realm of tasks analyzed here, the exclusive role of right AC seems to be the distinction of direction of continuous frequency changes. But it can also discriminate directions of stepped frequency change by disregarding the steps and creating a continuity illusion as recently shown in single-neuron responses recorded from macaque monkey's right auditory cortex (54). Thus, it seems to develop a rather global view of the frequency changes. The left AC can discriminate direction of frequency changes only if discrete steps are available for which it shows a fine discrimination, i.e., it seems to develop a directional discrimination from a local perspective of the time–frequency structure of such steps. Thus, our results support the view that auditory patterns are conceptually analyzed—comparable with visual patterns (47, 53, 55–58)—by local (sequential, analytic, relational) processing, preferentially in the left hemisphere, and/or global (parallel, holistic, unitary) processing, preferentially in the right hemisphere (52, 53, 59). This local/global interpretation should be confirmed by further animal studies, e.g., by experiments testing the smallest gap duration that would be sufficient for sequential processing or by experiments using the same stimuli that must be classified in different ways (44).

An implicit assumption of this characterization of right- versus left-AC discrimination functions derived from lesions is that under normal conditions these functions can be selectively used depending on the discrimination task rather than on the stimuli proper. There is no question from electrophysiological recordings that even simple neurons with a typical best frequency in the primary auditory cortex field (AI) of both right and left AC normally represent continuous and segmented FM in a tonotopically faithful activation pattern (47). But because only right AC seems able to explicitly distinguish a rising from a falling continuous FM, it must be assumed that an interaction with other parts of cortex that serve the behavioral consequences of this task is selectively established with right AC. This idea of flexible task-dependent interactions in cortex is much supported by human fMRI results (44, 45) and by anatomical evidence. Unlike subcortical auditory stations where processing steps can be explained by convergent and divergent ascending inputs, even primary AC receives >50% of its inputs from other cortical areas including many nonauditory fields (60). Thus, the

essence of cortical auditory processing is the top-down access to and interaction with other cortical functions that do not serve auditory analysis of sounds but rather their conceptualization and interpretation (47).

In principle, lesion studies in a sensory system cannot localize the emergence of a behavioral function to the lesioned level of the pathway. The crucial level or some preliminary mechanism of a function can always be more peripheral. Therefore, in some lesion cases, this more peripheral level may take over the function. This is likely the case in the present experiment 3 with discrimination of segmented from continuous FM (Fig. 3A and C). With bilateral or unilateral AC lesions alike, animals did not reach a normal high level of discrimination performance during the first block of training but improved upon additional training. Furthermore, animals lesioned after training only partially lost their discrimination performance (Fig. 3B, D, and E). These results are reminiscent of a previous AC-lesion study in gerbils in which animals first lost the discrimination of amplitude-modulated tones (20 vs. 40 Hz) but regained performance after additional training that was attributed to subcortical mechanisms of rhythm discrimination (61). Note that, in the present study, FM segmentation was equivalent to an amplitude modulation of sounds at 10 Hz. Thus, we hypothesize that subcortical levels of temporal processing of sounds are involved in the discrimination task of experiment 3. Future investigations, e.g., 2-deoxy-glucose imaging studies, are necessary, however, to determine what specific brain areas are activated in lesioned animals during temporal processing tasks.

In conclusion, the present data clearly demonstrate a cerebral lateralization of perception of artificial nonvocal sounds in a nonhuman species, i.e., in an auditory, not speech-specific model that separates basic auditory-level processing from speech- or vocalization-specific (phonetic-level) processing. These data suggest that asymmetries of auditory perception are not unique to humans nor are they specific to human speech or animal vocalization and further suggest that the asymmetries observed in a rodent species may represent critical evolutionary precursors to lateralized mechanisms for speech processing in humans. The various human studies, suggesting that common neurobiological mechanisms may underlie asymmetric cortical processing of both speech and nonspeech auditory stimuli, are complicated by the fact that perceiving speech represents the confluence of two separate tasks: recognizing both the acoustic characteristics and the semantic content of stimuli. Our study, however, provides a “prelinguistic” animal model suitable for the investigation of neurobiological mechanisms underlying normal and disturbed lateralized AC functions in humans.

Materials and Methods

Animals. We used 178 adult male Mongolian gerbils (*Meriones unguiculatus*) weighing 60–95 g. For details, see *Methods* in *SI Text*. All experiments were approved by the Ethics Committee of the State of Sachsen-Anhalt, Germany.

AC Lesions. Lesions were made under ketamine (100 mg/kg) and xylazine (5 mg/kg) anesthesia by thermocoagulation of the whole AC on the left side, or the right side, or bilaterally (Fig. 6); see *Methods* in *SI Text* for details.

Training Procedure. Gerbils were trained in a two-compartment shuttle-box (E10–15; Coulbourn Instruments) by using a go/no-go avoidance discrimination procedure (42); see *Methods* in *SI Text* for details.

Stimulus Characteristics. The digitally synthesized FM stimuli used as CS⁺ (go) and CS[−] (no-go) are shown in Table 1; see *Methods* in *SI Text* for details.

Evaluation of Results. Number of conditioned responses during CS⁺ (hits, CR⁺), number of conditioned responses during CS[−] (false alarms, CR[−]), response

latencies (times between CS onset and hurdle crossing), hurdle crossings during the intertrial interval, and intensity and duration of footshocks (unconditioned stimuli) were monitored and recorded by a custom-made computer program. The difference between counts of hits and false alarms (CR⁺ – CR[−]) was used as a measure of discrimination performance (CR difference). For statistical evaluation, see *Methods* in *SI Text*.

ACKNOWLEDGMENTS. We thank Lydia Löw, Ute Lerke, Kathrin Ohl, Elke Müller, Janet Stallmann, and Reinhard Blumenstein for skillful technical assistance, and Jason Shumake for revision of the English text. This work was supported by Deutsche Forschungsgemeinschaft Grant DFG SFB-TR 31, German Ministry of Science and Technology Grant BMBF BioFuture 0311891, and European Community Grant FP6-IST-027787.

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